THE DEVELOPMENT OF THE PENILE URETHRA IN THE PIG

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The mode of development of the penile urethra of the pig has been studied in order to discover whether the pattern of development in this animal is different from that described in man (Glenister, 1954). Ungulates are of special interest in this respect, as their penis becomes incorporated in the abdominal wall in the course of development.

LITERATURE

Although some of the earliest work on the development of the phallic region was carried out on human material by Tiedemann (1813), Meckel (1815) and Müller (1830), embryos from various species of ungulates have been used by several embryologists for the investigation of the development of this region. This was so presumably because this kind of material was available in abundance at a time when human embryos were difficult to obtain.

The three above-mentioned authors affirmed that the penile urethra was formed by the closure of a urethral gutter that extended along the under-surface of the penis. Rathke (1832) seems to have been the first author to become interested in the comparative aspects of the subject, and he stated that the closure of the urethral gutter to form the penile urethra starts at points which differ from mammal to mammal. Thus in rats the closure starts at the perineum, whereas in most ruminants it begins at the anterior extremity of the genital tubercle; in the pig the middle portion of the gutter is the last to close.

These classic descriptions were restated by Valentin (1835), Bischoff (1842), Koelliker (1861) and Cadiat (1884). The latter used mainly sheep embryos for his investigation, but also examined a limited number of pig and human embryos. He pointed out that the groove on the under-surface of the glans clitoridis and the vestibular region in the female correspond to the penile portion of the urethra in the male. Tourneux (1888), Fleischmann (1902–7), Schwartztrauber (1904), Böhm (1905) and Durbeck (1907) described the development of the external genitalia in sheep, pig, cat, guinea-pig and mole. These five authors state that the genital tubercle contains a low epithelial lamina (*lamina urethralis*), which protrudes into the mesoderm of the tubercle and is continuous caudally with the cloacal plug (*lamina cloacalis*). They do not state clearly what the role of the lamina urethralis is in the development of this region, but claim that the urorectal septum forms the perineum and the perineal raphe, and is thus responsible for the closure of the urethral groove. Thus, according to these authors, the urethral groove is not closed by the fusion in the midline of laterally placed urethral folds. The cranial displacement of the tip of the penis up to the umbilicus is explained by assuming that, in

male embryos, the perineum grows rapidly and is lengthened in a cranial direction to be incorporated in the abdominal wall.

Retterer (1890–1915) investigated the development of the urogenital system in horse, pig and sheep, as well as man, many rodents and many carnivores. His writings are so full of invective against Fleischmann and his school that it is often difficult to follow his arguments. He does, however, state quite clearly that the penile urethra results from the fusion of urethral folds, starting at the base of the organ and proceeding to the tip, this fusion giving rise to the perineal raphe. The urethral plate results from the outgrowth of urethral folds on either side of it and is definitely ectodermal in origin. Retterer does not, however, state clearly what part, if any, it plays in the formation of the urethra. This organ is, however, stated to be lined by epithelium derived from ectoderm and is formed throughout by the fusion of urethral folds. Retterer pours scorn on the concept presented by Wood Jones (1910) according to which the terminal urethra is derived from a separate ingrowth of ectodermal epithelium. It is, however, to Retterer's credit that he was not in the least impressed by the opinions of Felix (1912) which have so long formed the basis of accounts of the development of this region.

Retterer explained the close relation of the penile tip to the umbilicus in ungulates by describing a thickening of the abdominal wall extending from the linea alba to the penis. This thickening extends as a sling to the base of the free portion of the developing penis and so fixes it close to the umbilicus. Later a glando-preputial lamella grows in, separating the penis from the surrounding abdominal wall tissue, to give rise to an extensive preputial space. The free margin of the prepuce grows forward in the form of a preputial fold which gradually covers the whole of the free portion of the penis.

In 1924 Zietschmann stated that the cranial migration of the phallus is caused by the lengthening of the axial parts of the phallus underneath the perineal skin, the male genital tubercle of ungulates never developing into a cylinder which is free on all sides as in man. The enclosed main portion develops further, attached by means of connective tissue to the ventral abdominal wall.

In 1945, however, Broman compared the development of the penis in Primates with its development in Artiodactyla, and concluded that the penis which is enclosed in the abdominal wall is always developed ontogenetically from a *penis liber*, while the definitive penis liber never has a preliminary stage of being a *penis appositus*.

In 1947 the same author published a detailed account of the origin and secondary displacement of the external genitalia in ruminants, with special reference to the recognition of sex in pig, cow, sheep, roe deer, red deer and elk. This author describes a fusion of the urethral folds to form the penile urethra, and also describes a penile basal ring that anchors the base of the organ to the caudal part of the abdominal wall which in turn is drawn up towards the umbilicus. Thus the free portion of the penis is drawn cranially, the portion enclosed in the abdominal wall is greatly lengthened and the part of the penis that was at first free is completely drawn into the abdominal wall. Later this penile basal ring takes part in the formation of the definitive prepuce. Broman confined himself to the macroscopical appearances of the external genitalia and expressed no opinion about the origin and development of the urethral plate and urethra.

MATERIALS AND METHOD

The caudal parts of a series of thirteen pig foetuses ranging in size from 11 to 85 mm. crown-rump length, and the penis and abdominal wall of a pig foetus of 125 mm. crown-rump length, have been sectioned serially either in the coronal, the sagittal or the transverse plane. All specimens were measured after fixation, and were selected because the external genitalia presented either indifferent or male characteristics according to the criteria of Broman (1947). The sex of the foetuses was checked by means of the histological appearances of their respective gonads, the criteria of Gillman (1948) being applied.

DESCRIPTION OF MATERIAL

At 11 mm. the genital tubercle is barely identifiable with the naked eye and there are no genital swellings; the gonads are at the indifferent stage of differentiation.

The cloaca is an undivided cavity separated from the surface of the embryo by a thick cellular plate—the cloacal membrane. The urethral plate consists of a short cellular projection extending from the anterior wall of the cloaca and extending into the base of the phallic tubercle (Pl. 1, fig. 1). The constituent cells appear to be derived from the internal cloacal wall and to be distinct from the surface epithelium.

It should be noted that two sheep embryos of 13 and 15 mm. crown-rump length respectively were also examined, and showed quite clearly that the urethral plate consists of cells which are continuous with and indistinguishable, under the microscope, from those lining the internal cloacal or future urogenital sinus wall. In these two specimens the urethral plate is also quite distinct from the surface epithelium.

At 16 mm. the phallic tubercle of the pig embryo is in the form of a cone on to which ill-defined urethral folds extend from the margins of the ectodermal cloaca. The tubercle measured 1 mm. and no well-defined genital swellings were seen. The gonads are still at the indifferent stage of differentiation. The urethral plate extends along the under-surface and towards the tip of the phallic tubercle as a cellular proliferation from the anterior wall of the endodermal cloaca and urogenital sinus.

At 18 mm. the phallic tubercle is more elongated and measures 1·4 mm. The urethral folds are more clearly demarcated than in the 16 mm. specimen. No genital swellings have been observed and the gonad is still in the indifferent phase of differentiation. The urethral plate consists of a lamella extending into the phallus from, and derived from, the fused anterior portions of the walls of the urogenital sinus. The lower margin of the plate is in contact with surface epithelium which is two cells thick and which forms the roof of the ill-defined urethral groove. In the region of the tip of the phallus, the urethral plate extends to the dorsal surface of the tubercle. Where the urethral plate comes in contact with surface epithelium the plate tends to be thickened. The surface epithelium shows no sign of proliferation.

At 20 mm. the phallus is 1·5 mm. long and consists of a rounded knob situated

on a conical elevation. The urethral folds and groove extend on to the under-surface of both, and the tip of the knob is marked by a pit. Vague hillocks flanking the base of the phallic cone represent the primordia of the scrotal swellings. The gonads are early testes with well-defined sex cords and spindle-shaped cells under the coelomic epithelium forming the tunica albuginea.

The urogenital sinus and the rectum are completely separated, and the urethral plate extends into the phallus from the fused walls of the sinus. The dimple near the tip of the phallus indicates the site of an ingrowth of surface epithelium to meet the most anterior part of the urethral plate.

At 22 mm. the phallus measures 2 mm. A pit is again noted at the tip of the glans (Pl. 1, fig. 2), which is well defined in this specimen; the pit is in relation to the anterior extremity of the urethral groove. The genital swellings are poorly defined and situated on either side of the base of the phallus. The gonads can again be observed to be developing testes.

The definitive urogenital sinus is clearly divided into an antero-posteriorly compressed pars pelvina and a laterally compressed pars phallica. The urethral plate is formed from the fused walls of the urogenital sinus and is completely lamellar in form except for the deepest, most dorsal portion which is slightly thickened. The phallic portion of the urogenital sinus extends some way into this thickened part of the plate. This lamella lies in the roof of the groove produced by the bulging urethral folds (Pl. 1, fig. 3), and the surface epithelium in relation to the inferior margin of the plate is 'destratified' and appears to be retrogressing. Near the tip of the glans, the urethral plate forms a lamella occupying about two-thirds of the depth of the phallus. The urethral plate is quite distinct from the surface epithelium which is folded-in to meet the lower margin of the plate. These appearances probably result from the outgrowth of urethral folds on either side of the urethral plate. Sections through the tip of the phallus show that the terminal pit, already noted in the description of the external genitalia, is the site of an ingrowth of surface epithelium which meets the distal extremity of the endodermal urethral plate (Pl. 1, fig. 4).

At 25 mm. the phallus is curved caudalwards and is 2·5 mm. long. The primitive urogenital ostium is visible at the base of the phallus and is continuous with the urethral groove which is deeper in its proximal portion. The groove becomes progressively shallower as it is traced towards the tip of the phallus which is surmounted by a globular glans. The urethral folds flank the primitive urogenital ostium and the urethral groove, which is continued on to the under-surface of the glans, whence it may be traced to a definite pit near the summit of the organ. There is no vestige of an epithelial tag. The scrotal swellings are now quite evident and are situated in relation to the cranial part of the base of the phallus.

At 27 mm. the external genitalia present the same features except that the phallus is more markedly curved, so that the distal half is set at right angles to the proximal half (Pl. 1, fig. 5).

As these two stages present such similar appearances it is convenient to describe their histological features together.

The gonads are early testes and the pelvic and phallic portions of the urogenital sinus are clearly defined in both foetuses. The lumen of the phallic portion opens

out on to the surface at the primitive urogenital ostium, and this in turn is continuous with the urethral groove (Pl. 1, fig. 8). The part of the urethral groove immediately in front of the ostium is formed by the outgrowth of urethral folds lined by surface epithelium as in the previous cases, but it is deepened by the disintegration of the lower (ventral) thickened part of the urethral plate. The site of the latter is still indicated by epithelial bridges (Pl. 1, fig. 7). Farther forward along the phallus, the urethral groove is shallower (Pl. 1, fig. 6), the urethral plate is lamellar in outline and the surface epithelium, lining the roof of this part of the groove and in relation to the lower margin of the plate, gives the appearance of retrogressing, being 'destratified' and stretched out. As sections are traced towards the tip of the phallus, it is found that the epithelium lining the urethral groove is composed of as many layers of cells as are found in the epithelium lining the other surfaces of this region of the phallus. At the tip, an ingrowth of cells derived from the surface epithelium meets the distal part of the urethral plate. It has not been possible to determine in these specimens whether there is an additional ingrowth of surface cells from the terminal part of the urethral groove to meet the terminal part of the urethral plate, or whether the apparent infolding of surface epithelium is due to the outgrowth of the urethral folds.

At 32 mm. the phallus is 2·5 mm. long and has a distinct curvature in a caudal direction (Pl. 1, fig. 11), but it is not so marked as in the 27 mm. specimen. The distal limit of the urogenital ostium has extended to half-way along the under-surface of the shaft of the phallus, while the proximal part of the ostium appears to have been closed by the fusion of the urethral folds. The summit of the glans is marked by a clearly defined pit. The scrotal swellings are hemispherical and are situated one on either side of the midline just cranial to the base of the phallus. The developing testes now contain easily identifiable, eosinophilic interstitial cells, a feature that was absent in the younger specimens.

Cellular buds extending from the lateral walls of the phallic part of the urogenital sinus have appeared. These are the bulbo-urethral gland rudiments, and they originate from the lining of the phallic portion of the urogenital sinus close to its junction with the pelvic part.

The urogenital ostium is still in relation to the most anterior portion of the pars phallica, the epithelial lining of which is very thickened. The urethral folds have fused to close the most caudal part of the pars phallica, thus forming the proximal part of the penile urethra. Owing to the obliquity of the sections, it is possible to confirm that the deeper part of the urethral groove along the shaft of the phallus is formed by the disintegration of the thickened ventral part of the urethral plate. The urethral plate extends into the glans, but does not quite reach the tip, as a short cellular cord of cells derived from the surface epithelium lining the pit on the summit meets the anterior extremity of the urethral plate.

At 35 mm. the external genitalia and their histological picture are very similar to those seen at the 38 mm. stage, and these two stages may be described together. The phallus is bent to a right angle and is 3 mm. long (Pl. 2, fig. 22). The most caudal part of the urethral groove has been closed by fusion of the urethral folds, so that the urogenital ostium has been displaced distally along the under-surface of the developing penis and opens into the proximal end of the urethral groove.

The proximal limit of this groove is situated at about a third of the way along the shaft of the phallus and is wide and deep. This wide and deep portion of the groove is continued on to the under-surface of the proximal part of the glans, and from there on the groove becomes narrower and shallower as it is traced towards the terminal pit near the summit of the glans.

In previous specimens, the part of the abdominal wall between the base of the developing phallus or penis was more or less translucent and consisted of surface epithelium covering loose mesenchyme. The corresponding region in these foetuses is more or less equally divided by a raised crescentic margin disposed transversely to the cranio-caudal axis of the foetus. The part of the developing penis containing the formed (closed) portion of the penile urethra is seen to be attached to the ventral abdominal wall caudal to the crescentic margin. Thus the shaft of the penis has begun to be incorporated in the abdominal wall, and as its free portion is being drawn towards the umbilicus the genital swellings have come to lie caudal to the base of the free portion of the phallus.

In the testes of both specimens the interstitial cells are large, very well defined and eosinophilic.

The phallic portion of the urogenital sinus, the lining epithelium of which is many cells thick, and the proximal part of the urethral groove have been closed and converted into a tube by fusion of the urethral folds in the midline. The resulting raphe is indicated on the surface by a ridge. The folds fuse in such a way that epithelium derived from the sinus or the urethral plate forms the lining of the resulting urethra, and surface epithelium is excluded except possibly from its floor (Pl. 1, fig. 10). The proximal portion of the urethral groove is lined by epithelium derived from the lower basal part of the urethral plate (Pl. 1, fig. 12). The site of junction with surface epithelium is indicated by a heaping up of cells inside the free margin of the urethral folds. In the glans the urethral plate is met by an ingrowth of surface cells along the under-surface of the glans. The site of junction of the two types of epithelium results in a proliferation, which by breaking down gives rise to the distal part of the urethral groove (Pl. 1, fig. 12), which is encroaching on the glans of both specimens. The ingrowth of surface cells referred to above is continuous with the cord of cells which grows in from the terminal pit (Pl. 1, fig. 10) to reach the distal part of the urethral plate.

Sections through the abdominal wall show that the crescentic margin, described in conjunction with the appearances of the external genitalia, is the surface indication of the inner limit of the caudal part of a ring of differentiating subcutaneous muscle. This ring is disposed around the attachment of the umbilical cord to the abdominal wall, but the ring is still separated from the cord by a wide cuff of loose mesenchyme. The subcutaneous muscle ring is the developing umbilical sphincter, and it lies superficial to the differentiating abdominal subcutaneous muscle sheet. The formed parts of the developing penis are closely attached to the developing sphincter, the junctional region being marked by numerous capillaries (Pl. 2, fig. 17).

At 45 mm. the penis is clearly subdivided into two unequal parts (Pl. 2, fig. 23), the total length being about 7 mm. The larger segment comprises that part of the penis which is enclosed in the body wall, the smaller segment is free and recurved

and consists mainly of an elongated glans; a fold of skin extends round the back and sides of its base. The extent of the larger 'pars captiva' is indicated on the surface by a median raphe. The base of the 'pars liber' is situated half-way between the scrotal swellings and the attachment of the umbilical cord. The free portion of the penis is so recurved that it is impossible to see where the urinary meatus is situated. The raised margin on the caudal part of the abdominal wall of the previous two specimens consisted of an arc of a circle around the umbilical cord. The corresponding margin in the 45 mm. foetus, although still separated from the umbilical cord by a depressed area 1 mm. wide, encircles the attachment of the cord to the abdominal wall completely. The fold of skin surrounding the base of the free portion of the penis joins the latter to the most caudal point on the circumference of the raised margin. The fold corresponds to the penile basal ring described in various ungulate foetuses by Broman in 1947.

The epithelium lining the part of the urethra derived from the urogenital sinus is still very thick, and the bulbo-urethral gland rudiments now consist of a solid duct leading to ramifying cellular buds. The duct joins the proximal part of the penile urethra near its junction with the membranous urethra (Pl. 1, fig. 9). The penile urethra is fully formed as far as the glans except for the persistence of the urethral plate in the roof of the most distal part. The line of fusion of the urethral folds is indicated by a fibrous condensation extending from the floor of the urethra to the thickened raphe on the surface of the foetus. The urinary meatus is situated on the under-surface of the glans. The roof of the proximal part of the urethral groove and the most distal part of the formed urethra are lined by epithelium derived from the urethral plate (Pl. 2, figs. 13, 14). This epithelium is less thick than that lining the parts of the urethra derived from the phallic part of the urogenital sinus. Along the inner surface of the urethral folds, the junction between surface epithelium and epithelium derived from the urethral plate is indicated by a heaping up of epithelial cells. Closure of the folds may result in the inclusion of some surface cells in the lining of the floor of this portion of the urethra, where the epithelium is many cells thicker than in the roof. The urethral plate extends into the proximal portion of the glans and the ventral (superficial), reactive, thickened part of it breaks down and leaves epithelial bridges across the resulting groove. The dimensions of the surface ingrowth to meet the distal part of the urethral plate have increased greatly, and the reactive proliferation at this junctional region is breaking down to form the most distal part of the urethral groove (Pl. 2, fig. 15).

Although it was not evident to the naked eye, examination of sections through the penis shows that a preputial fold has appeared round the base of the glans, and it lies within the inner surface of the penile basal ring (Pl. 2, fig. 18). Muscle fibres are differentiating to form a fibromuscular sling connecting the umbilical sphincter to the deep aspect and sides of the distal end of the enclosed part of the penis. This sling also extends round the sides of the penis to reach the penile basal ring and the preputial fold.

At 65 mm. the penis has been drawn up to within 1 mm. of the umbilical cord, apparently by the contraction of the umbilical sphincter which invests the cord fairly closely. The penis is 10 mm. long and only the terminal 1 mm. is recurved

and free. The median raphe forms a distinct ridge on the surface of the embryo and overlies the enclosed portion of the penis.

The penile urethra has been formed as far as the proximal part of the glans on whose under-surface the urinary meatus is situated near the tip of the organ. There is no sign of a urethral plate in this specimen, but the epithelium lining the proximal and distal parts of the penile urethra is thicker than in previous specimens. The surface ingrowth from the tip of the glans is a well-formed lamella, the ventral and superficial part of which gives rise to the terminal part of the urethra.

There is a well-developed glandar lamella which grows in alongside the part of the glans which is already enclosed in the abdominal wall. The deeper parts of the lamella are more cellular and less well differentiated than the more superficial parts. The preputial fold and the penile basal ring have merged to form one fold surrounding the superficial part of the glandar lamella. A preputial diverticulum, which possesses a lumen, extends dorsal to the glans from the superficial part of the glandar lamella.

At 85 mm. the penis has been drawn up to the umbilicus (Pl. 2, fig. 24), and the scrotal swellings have migrated caudally to lie just cranial to the anus; they are unfused. The glans of the penis is almost completely covered by the prepuce and a surface indication of the underlying umbilical sphincter is only just visible.

The proximal part of the penile urethra, i.e. the part formed from the phallic portion of the urogenital sinus, is dilated and has a considerably wider lumen than that of the remainder of the penile urethra; its lining epithelium is also stratified to a greater extent. The glandar urethra has been formed to the very tip of the glans. The terminal part of the urethra is derived from the surface ingrowth which grew in to meet the distal part of the urethral plate, which has however disappeared. The ingrowth is lamellar in form but, owing to the twisting of the apical part of the glans, the lamella has also got twisted and the histological picture is somewhat confused. However, it can be seen that it is the superficial basal part of the lamella from which the terminal urethra is derived. The stratified epithelium lining the distal part of the glandar urethra is many cells thick and is similar to and continuous with the epithelium covering the surface of the glans (Pl. 2, fig. 16). The greater distal part of the glandar urethra appears to be lined by this type of epithelium.

The preputial diverticulum opens into the most cranial portion of the preputial furrow. The terminal part of the glans lies twisted within the preputial space which appears to form without the formation of 'epithelial pearls', which are so prominent in the glandar lamella of man. Nor have epithelial pearls been noted in the formation of the glandar urethra, cf. man (Glenister, 1954). The deepest part of the glandar lamella is made up of cells which appear to be less differentiated than those constituting the more superficial parts of the lamella and thus gives the impression of still growing in.

The muscular sling which surrounds the distal part of the enclosed portion of the penis in this specimen, as in the previous two, connects this part of the penis to a ring of muscle around the umbilical cord (Pl. 2, fig. 19).

A dissection of the peri-umbilical region of a 125 mm. foetus and serial sections through the corresponding region of another foetus of the same size, show that

the terminal portion of the penis, which is now completely enclosed within the abdominal wall, is attached to the umbilical sphincter (Pl. 2, fig. 21). The latter lies subcutaneously and forms a sling passing caudal to the umbilical cord and extending cranially as two muscular columns (Pl. 2, fig. 20), flanking either side of the umbilicus to be attached to the cranial portion of the linea alba. Muscle fibres can be traced from the caudal part of the umbilical sphincter to the prepuce, and to the sides of the penis; some extend round the latter to reach the penile raphe.

It should be noted that the cranial portion of the umbilical sphincter lies superficial to the subcutaneous abdominal muscles, and that these two muscles lose their intimate relation to the sphincter caudal to the umbilicus as they diverge towards the region of the stifles.

Although the sphincter and the subcutaneous muscles are attached to the cranial part of the linea alba, they are otherwise superficial to and quite distinct from the rectus sheaths (Pl. 2, fig. 21).

Dissection of the abdominal wall of a near-term foetus shows that the same topographical relations exist up to the time of birth.

DISCUSSION AND CONCLUSIONS

It is evident from this study that although the penis of the pig becomes incorporated in the abdominal wall in the course of development, the penile urethra is formed in a way that is essentially similar to that taking place in man.

The urethral plate develops as a lamellar outgrowth from the fused anterior walls of the cloaca and urogenital sinus. The plate is not, as suggested by Retterer (1914), the product of an outgrowth of urethral folds on either side of a median strip of surface epithelium, continuous with the cloacal membrane. This fact is emphasized by the observation that the urethral plate is recognizable as a well-defined lamella in the 11, 16 and 18 mm. pig embryos; the urethral folds, however, are not clearly seen on the surface till the 20 mm. stage. Although essentially similar to the urethral plates observed in human foetuses, the plates described in these pig foetuses do not extend so deeply into the mesenchyme of the developing penis and thus appear shorter in transverse section.

As may be appreciated from a review of the literature, few, if any, of the authors have studied the details of the formation of the urethral groove in man or in animals, and they seem to have dismissed it as resulting quite simply from the outgrowth of urethral folds on either side of the midline (Debièrre, 1883; Retterer, 1890–1915; Fleischmann, 1902–7; Tourneux, 1889; Schwartztrauber, 1904; Böhm, 1905; Lichtenberg, 1906; Paschkis, 1906; Johnson, 1920; Spaulding, 1921).

Herzog (1904) implied that it was formed by a splitting of the urethral plate, and only gave rise to the urethra of the glans. Felix (1912) held the same opinion. Van den Broek (1909, 1910) also considered that the superficial part of the urethral plate splits but contributes to the lining of all parts of the urethral groove. Williams (1952) describes a urethral groove on the glans analogous to that of the shaft and derived in part by the 'opening up' of the urethral plate and in part from epidermis.

In fact, the urethral groove is formed in the pig by the same complicated processes

as already described in man (Glenister, 1954). The processes start at the base of the phallus and then extend distally towards the tip. Urethral folds grow out on either side of the urethral plate and on either side of the phallic part of the urogenital sinus, thus forming the *primitive* or *primary urethral groove.* This groove is continuous caudally with the primitive urogenital ostium. The lower, superficial margin of the urethral plate becomes thickened as the surface epithelium in relation to it appears to disintegrate. In turn, this thickening of the urethral plate is followed by a disintegration of the thickened portion to form a *secondary urethral groove.* The combined product of primary and secondary urethral grooves may be termed the *definitive urethral groove.*

However, in the pig foetuses examined, the surface epithelium in contact with the basal margin of the urethral plate, in the roof of the urethral groove, has never been observed to be proliferating before retrogressing and breaking down. This provides an explanation for the fact that no terminal epithelial tags, so prominent in human specimens, have been observed in pig foetuses.

As in man, closure of the urethral folds related to the phallic part of the urogenital sinus gives rise to the proximal dilated portion of the penile urethra, while the remainder of the urethra of the shaft of the penis and of the proximal part of the glandar urethra is formed by the fusion of the part of the urethral folds related to the definitive urethral groove. The fusion of the urethral folds takes place in such a way that surface epithelium is excluded from the lumen of the greater part of the penile urethra. Near the tip of the penis surface epithelium is incorporated into the lining of the floor of the urethra, while the terminal portion of the urethra is derived entirely from surface epithelium which grows in to meet the distal extremity of the urethral plate.

Fusion of the urethral folds gives rise to the perineal raphe. The formation of this structure was described correctly by Retterer (1890–1914), and no evidence has been found to support the views of Tourneux (1888, 1889) and Fleischmann (1902–7) and their respective schools. It should also be noted that the fusion of the urethral folds starts caudally and proceeds towards the tip of the phallus, there being again no evidence to support the views of Rathke (1832).

Attention has already been drawn to the fact that no terminal epithelial tag has been observed in any of the pig foetuses examined. Instead, a terminal pit, which is continuous with the distal part of the urethral groove, appears at about the 20 mm. stage and an epithelial ingrowth, derived from the lining of this pit and the distal part of the urethral groove, grows into the substance of the glans to meet the distal extremity of the urethral plate. In the previous publication dealing with the development of the penile urethra in man it was stated that when the ectodermal epithelium breaks down after proliferation, it does so by passing through a phase of 'epithelial pearl' formation, whereas the urethral plate proliferation breaks down, leaving 'epithelial bridges' across the resulting groove. The latter phenomenon has also been observed in the pig, but the former was absent both in the ingrowth forming the terminal urethra and in the glandar lamella, and could not be used as a criterion of surface origin.

As regards the formation of the prepuce it would appear to start soon after the 40 mm. stage (a preputial fold is present in the 45 mm. specimen) at which stage

the glans is quite free from the abdominal wall. By the 65 mm. stage, the glans has been partly incorporated into the abdominal wall and the processes of prepuce formation are thereby obscured. However, the glandar lamella is well developed by this stage, and at the 85 mm. stage, when the deeper portions of the lamella still appear to consist of less well-differentiated ingrowing cells. It seems therefore that, in the pig, the prepuce results from a combination of preputial fold formation and ingrowth of a glandar lamella; in other words, by processes essentially similar to those taking place in human foetuses (it is hoped to publish a note on the development of the prepuce in man at a later date).

Thus the views expressed here concur with those of Retterer (1890–1915), who believed that prepuce formation results from a combination of preputial fold and glandar lamella formation. It may be added that the observations described in this paper could not be interpreted satisfactorily were the prepuce to result from preputial fold formation only, as claimed by Berry Hart (1908) and Hunter (1935), or to result entirely from the ingrowth and subsequent splitting of the glandar lamella as described by Böhm (1905), Wood Jones (1910) and Johnson (1920).

The incorporation of the penis in the abdominal wall and the drawing up of the penile tip to the umbilical region would seem to result from an early association of the formed parts of the penis with the developing umbilical sphincter. The onset of the process of incorporation coincides with the appearance in the abdominal wall of a subcutaneous umbilical sphincter to which the formed part of the penis becomes attached by a fibromuscular sling. This sling extends from the most caudal part of the sphincter to the sides of the penis and to the line of fusion of the urethral folds. As the muscle ring constituting the sphincter comes to encircle the attachment of the umbilical cord more closely, the distal end of the formed part of the penis is drawn forward progressively so that the tip ultimately lies just caudal to the umbilicus. As well as extending round the sides of the penis to reach the line of fusion of the urethral folds, the fibromuscular sling connecting the penis to the umbilical sphincter can also be traced to the preputial fold and the penile basal ring when these structures appear. Broman (1947) claimed that this penile basal ring connected the base of the free portion of the developing penis to a margin raised by the inner edge of the developing rectus muscles and that the basal ring was responsible for drawing up the penile tip to the umbilicus. It must be pointed out that Broman only examined his material macroscopically. When ungulate foetuses are sectioned and examined microscopically, it becomes obvious that the raised margin is the surface indication of the underlying umbilical sphincter, and that the penile basal ring is a cutaneous fold to which some of the fibres of the connecting sling are attached. This fold later merges with the preputial fold to form the superficial distal part of the prepuce, which is drawn over the tip of the penis when the latter becomes completely enclosed in the abdominal wall.

It should be noted that all the while part of the urethral groove remains open, the penile basal ring and preputial fold remain caudal to the open part of the groove and the urogenital ostium which opens into it. In other words, the successive parts of the penis are incorporated into the abdominal wall only after the part of the urethra related to them has been formed.

Thus Zietschmann's account (1924), describing the cranial migration of the

phallus as being caused by a lengthening of the axial parts of the organ under the perineal skin, is not accurate.

The bulbo-urethral glands of the pig develop, as in man, as cellular outgrowths from the phallic part of the urogenital sinus near its junction with the pelvic portion.

This study may thus be said to indicate that an ungulate such as the pig develops its penile urethra by processes essentially similar to those taking place in man, but complicated by the attachment of the penis to an umbilical sphincter, a structure not found in human foetuses (Parry, 1954).* The uniformity of the pattern of urethral development described here conforms to the view of Retterer (1914), who stated that all mammals develop their external genitalia according to the same basic plan.

In conclusion, attention must be drawn to the marked proliferation and stratification observed in the lining epithelium of the parts of the urethra developed from the urogenital sinus and in the glandar urethra, whereas the intermediate portion shows no such phenomenon.

The proliferation is very reminiscent of that described by Zuckerman (1940), Moore (1941) and Burns (1942), in connexion with the modifications induced by oestrogens in epithelium derived from the urogenital sinus. The proliferation observed in the present series, as also in the untreated specimens described by Burns, could conceivably be due to the oestrogens of the mother. It is, however, difficult to understand why, on the one hand, a lining epithelium derived from the surface of the embryo and one derived from the urogenital sinus should react, whereas the intermediate portion derived from the urethral plate and so also ultimately from the sinus, does not. The possibility that the response to oestrogens is not as specific as suggested by Zuckerman (1940) and Burns (1942) must be envisaged.

It must be conceded to these authors when considering from which germ-layer the lining of the urogenital sinus and the urethral plate are derived, that the possibility exists that ectodermal cells may be incorporated in their formation. The cloacal membrane gives rise to the floor of the urogenital sinus, and may possess a degree of plasticity which enables ectodermal cells to migrate to the deeper part of the membrane and so become incorporated in the primarily endodermal lining of the sinus. This incorporation must, however, take place very early in development, before the breaking down of the cloacal membrane and not after this, as suggested by Burns (1942). The replacement of one type of epithelium by another, which he observed in his experimental material and suggested took place in normal foetuses after the breakdown of the membrane, has not been observed in either man or the pig.

* Hauptmann (1911) described an umbilical sphincter in the horse, and Parry (1954) described this structure in the cow, sheep, rabbit and guinea-pig. She noted the absence of the sphincter in man, macaque, rat, dog, cat and pangolin. She stated that her preliminary observations indicated the presence of an umbilical sphincter in the pig. As the result of this investigation it is confirmed that the pig possesses this structure, and dissection of near-term foetuses shows that the deer and the springbok may be added to the list of mammals possessing an umbilical sphincter. In their case, as in the case of the cow, sheep and pig, the terminal part of the penis and the prepuce are attached to the sphincter.

The suggestion that the distal part of the urogenital sinus is histogenetically related to ectoderm and that there may be a tendency for these distal ectodermal components of the sinus to impress their character on the proximal endodermal tissue (Zuckerman, 1940) is based on the accounts of Keibel (1910), Pohlman (1911), Lewis (1912), Keith (1923) and Frazer (1931), according to which the cloacal membrane incorporates part of the primitive streak. As the streak is considered to be the homologue of the blastopore of lower forms, the cloacal zone is looked upon as a region which, in an earlier phase of its development, was the centre of formative movements of the body and where cells streamed in from the surface of the embryo to deeper structures.

Attractive as this hypothesis may be when seeking an explanation for the results of experimental embryology, it must be remembered that in the first place the cells which stream in from the surface in the region of the primitive streak are cells giving rise to mesodermal components. Secondly, Florian (1930, 1933, 1934) and Wyburn (1937) have demonstrated that, at any rate in man, the cloacal membrane is not a secondary formation, but that the fusion of ectoderm and endoderm at the caudal end of the embryonic shield occurs as early as, if not before, the appearance of the primordium of the primitive streak. According to these authors, the streak represents the fused lips of the blastopore, the cloacal membrane being the homologue of the ventral lip of the blastopore and the adjacent area. Neither author mentions any streaming in of surface cells to deeper structures within the confines of the cloacal membrane. Wyburn considers, further, that the cloacal membrane is not so much a development as an actual persistence of contact between ectoderm and endoderm, the contact not being disturbed by mesoderm passing round the membrane towards the body stalk from the primitive streak. According to this author the streak ends at or short of the cloacal membrane.

SUMMARY

1. A series of pig foetuses ranging in size from 11 to 125 mm. crown-rump length has been examined to ascertain whether incorporation of the penis in the abdominal wall affects the processes of development of the penile urethra.

2. The penile urethra of the pig has been found to develop by processes essentially similar to those already described by the author in man.

3. The drawing forward of the penile tip to the umbilical region is effected by a fibromuscular attachment of the distal part of the penis to the umbilical sphincter.

4. The relative importance of the contributions of ectoderm and endoderm to the urethral lining is discussed.

I wish to acknowledge the encouragement and constructive criticism received from Prof. W. J. Hamilton. I am indebted to Mr R. H. Watts for his technical assistance and to Mr R. J. McCulloch for the photography.

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EXPLANATION OF PLATES

List of abbreviations

B.R.	penile basal ring	*P.Ph.*	phallic portion of the urogenital sinus
B.U.	bulbo-urethral gland rudiment	*R.P.*	reactive proliferation
Cl.	cloaca	*R.S.*	rectus sheath
E.J.	junction of surface epithelium with epithelium derived from the urethral plate	*S.E.*	surface epithelium
		S.G.	secondary groove
		S.M.	subcutaneous muscle
F.P.	free portion of the penis	*T.P.*	terminal pit
G.L.	glandar lamella	*U.F.*	urethral fold
I.E.	ingrowth of surface epithelium	*U.G.*	urethral groove
L.A.	linea alba	*U.O.*	urogenital ostium
M.S.	muscular sling	*U.P.*	urethral plate
P.F.	preputial fold	*Ur.*	urethra
P.G.	primary groove	*U.S.*	umbilical sphincter
P.Pe.	pelvic portion of the urogenital sinus	*U.V.*	umbilical vessels

PLATE 1

Fig. 1. Transverse section through the cloacal region of the 11 mm. pig embryo. The urethral plate is seen to be formed from the converging walls of the cloaca. × 120.

Fig. 2. The external genitalia of the 22 mm. pig foetus, showing the urethral groove on the undersurface of the phallus, and the terminal pit. × 4·5.

Fig. 3. Transverse section through the phallus of the 22 mm. foetus, showing that the urethral plate is distinct from the surface epithelium. The latter is thinned out and retrogressing in relation to the basal portion of the urethral plate. The primary urethral groove is flanked by urethral folds. × 87.

Fig. 4. Oblique section through the tip of the phallus of the 22 mm. foetus, showing the ingrowth of surface epithelium from the terminal pit to meet the distal extremity of the urethral plate. × 87.

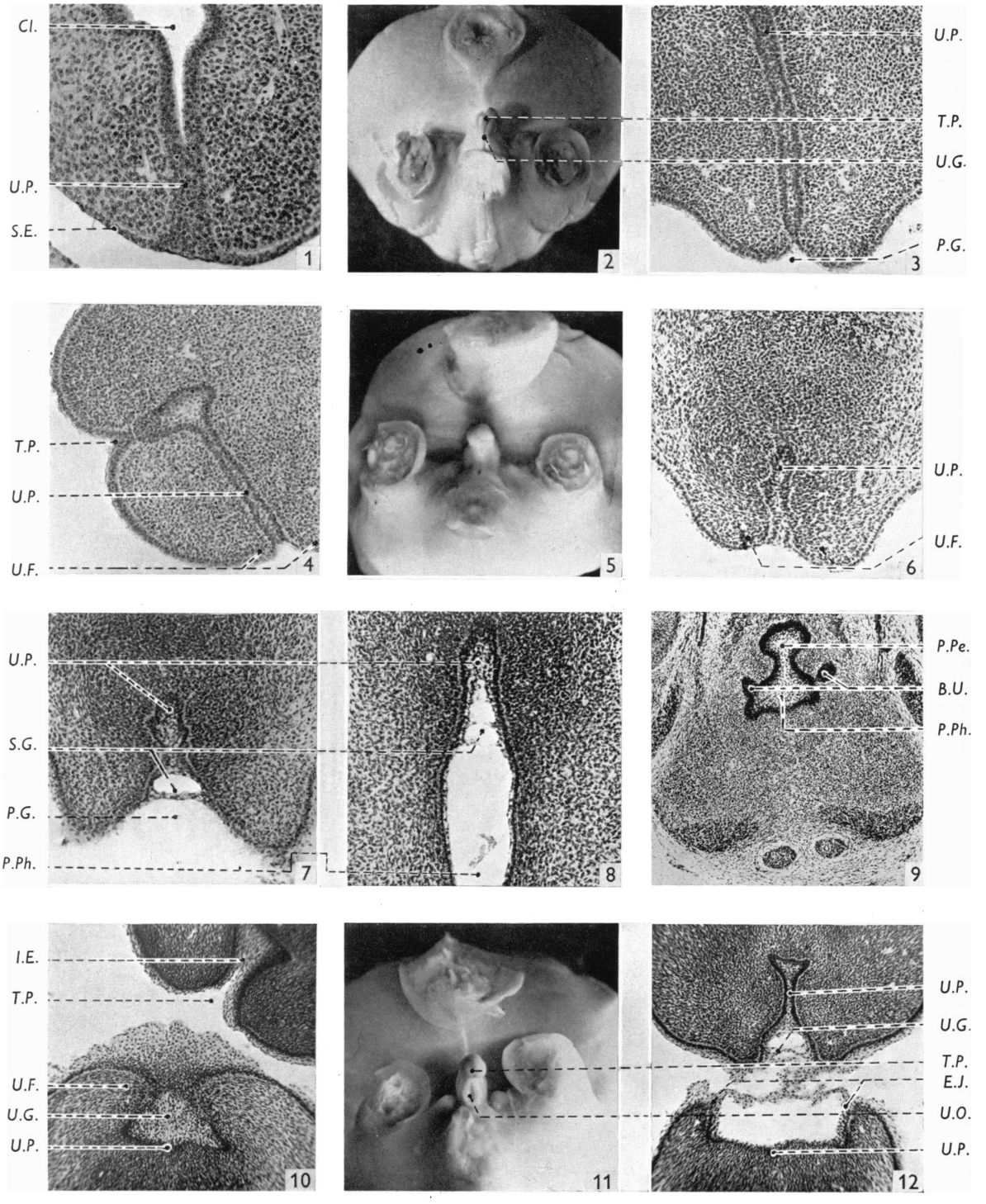
Fig. 5. The external genitalia of the 25 mm. foetus, showing that the proximal end of the urethral groove is deeper than the distal portion. × 4·5.

Fig. 6. Transverse section through the distal part of the shaft of the phallus of the 27 mm. foetus. The urethral plate is lamellar in shape, and the surface epithelium lining the primary urethral groove in relation to the lower margin of the plate is thinned out. × 87.

Fig. 7. Transverse section through the proximal part of the phallus of the 27 mm. foetus, showing that the basal part of the urethral plate is thickened and disintegrating. The resulting secondary groove has epithelial bridges extending across it, and it deepens the primary groove which is lined by surface epithelium. × 75.

Fig. 8. Coronal section through the caudal parts of the 27 mm. foetus, showing (from above downwards) the urethral plate, the most caudal part of the secondary urethral groove and the phallic part of the urogenital sinus. × 75.

Fig. 9. Coronal section through the junction of the pelvic and phallic portions of the urogenital sinus of the 45 mm. foetus. The bulbo-urethral gland rudiments are seen extending from the phallic part. × 48.



GLENISTER—THE DEVELOPMENT OF THE PENILE URETHRA IN THE PIG

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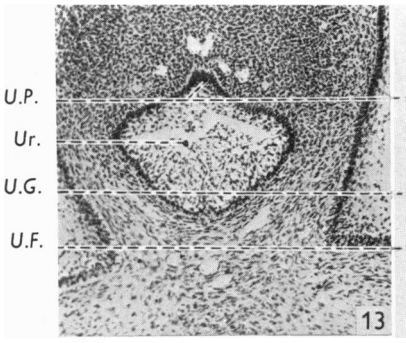
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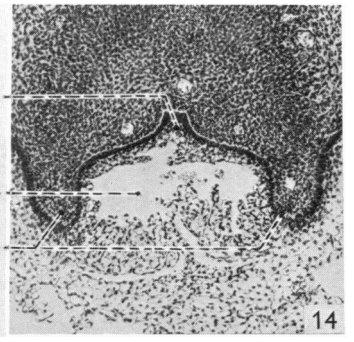
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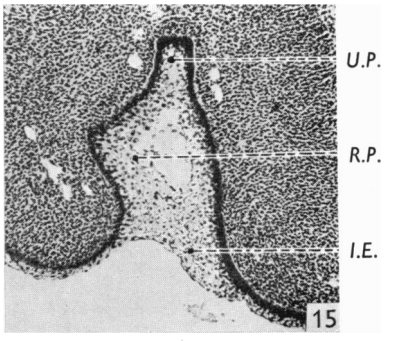
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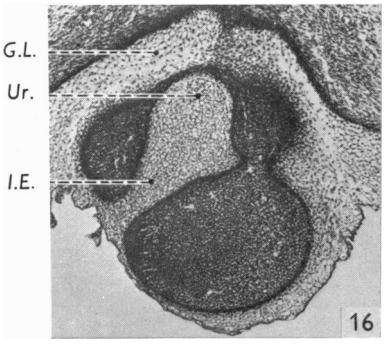
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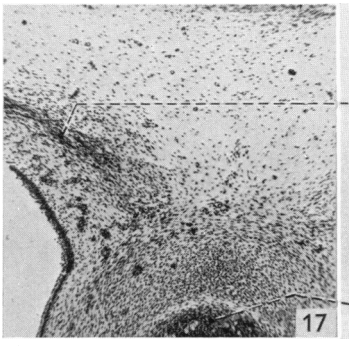
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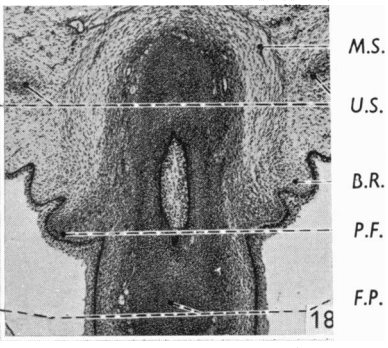
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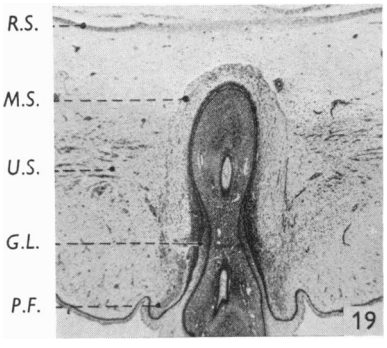
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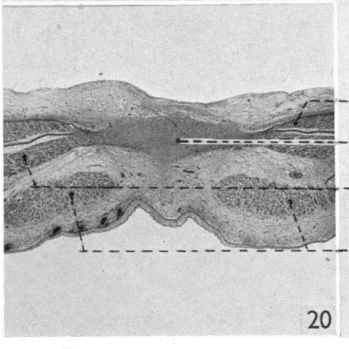
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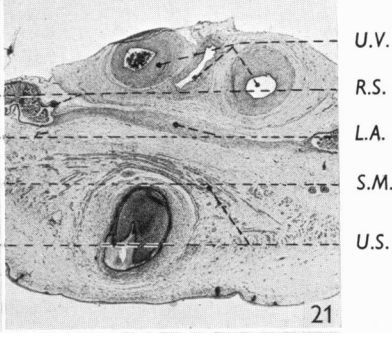
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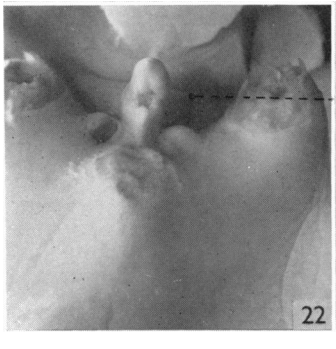
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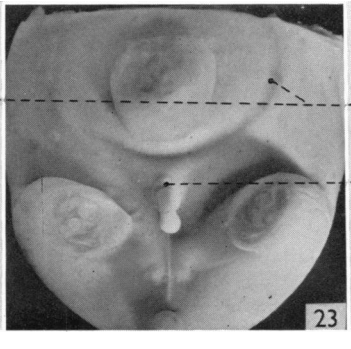
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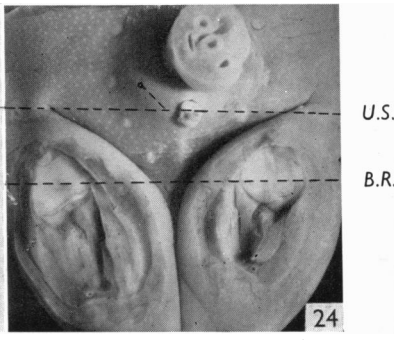
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Fig. 10. Transverse section through the curved phallus of the 35 mm. foetus. The distal segment is seen in the upper part of the figure, and it shows the ingrowth of surface epithelium from the terminal pit. In the proximal segment, the urethral folds are seen approaching one another to convert the urethral groove into a tubular urethra. × 60.

Fig. 11. The external genitalia of the 32 mm. foetus. The urethral folds have fused to close the most caudal portion of the phallic part of the urogenital sinus. As the result of this, the urogenital ostium is no longer situated at the base, but now opens on the under-surface of the phallus. × 4·5.

Fig. 12. Transverse section through the curved phallus of the 35 mm. foetus. The distal segment is seen in the upper part of the figure and shows the reactive proliferation at the lower margin of the urethral plate, breaking down to give rise to the urethral groove on the glans. The urethral groove on the shaft of the phallus (lower part of figure) is lined by cells derived from the urethral plate. The junction of this type of epithelium and surface epithelium is indicated by a heaping up of cells. × 60.

PLATE 2

Fig. 13. Transverse section through the distal part of the formed penile urethra of the 45 mm. foetus. The remains of the urethral plate are seen in the roof of the urethra. × 90.

Fig. 14. Transverse section through the urethral groove of the 45 mm. foetus. Only the roof of the groove is lined by cells derived from the urethral plate. × 90.

Fig. 15. Transverse section through the distal part of the penis of the 45 mm. foetus, showing the reactive proliferation at the junction of the urethral plate and surface ingrowth. The proliferation is breaking down to give rise to the most distal part of the urethral groove. × 90.

Fig. 16. Transverse section through the distal part of the penis of the 85 mm. foetus, showing that the lining of the terminal part of the urethra is similar to and continuous with the superficial lining of the penis and the glandar lamella. × 45.

Fig. 17. Transverse section through the distal part of the enclosed portion of the developing penis of the 38 mm. foetus. The region of attachment of the penis to the developing umbilical sphincter is marked by numerous arterioles and capillaries. × 39.

Fig. 18. Transverse section through the junction of the free and enclosed parts of the penis of the 45 mm. foetus. The preputial fold and the penile basal ring outside it are seen flanking the base of the free portion of the penis. A fibromuscular sling joins these cutaneous folds and the sides of the penis to the developing umbilical sphincter. × 36.

Fig. 19. Transverse section through the distal part of the penis of the 85 mm. foetus, showing the relations of the penis and fibromuscular sling to the umbilical sphincter and of the latter to the rectus sheath and linea alba. × 15.

Fig. 20. Transverse section through the abdominal wall of the 125 mm. foetus, showing the relations of the umbilical sphincter to the subcutaneous muscle sheet, the rectus sheath and the linea alba. × 12.

Fig. 21. Transverse section through the abdominal wall of the 125 mm. foetus at a level which is caudal to that of Fig. 20. This figure shows the relations of the terminal portion of the penis to the umbilical sphincter. × 12.

Fig. 22. The external genitalia of the 38 mm. foetus. The proximal part of the penis has become attached to the abdominal wall. The junction between the free and attached portions of the penis is connected to the margin raised by the underlying developing umbilical sphincter. × 4·5.

Fig. 23. The external genitalia of the 45 mm. foetus showing the penile basal ring connecting the base of the free portion of the penis to the margin raised by the developing umbilical sphincter. × 3·6.

Fig. 24. The external genitalia of the 85 mm. foetus showing that the umbilical sphincter encircles the umbilical cord closely and has drawn up the penile tip to within a fraction of a millimetre caudal to the cord. × 3·6.